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# Worker populations of *Formica lugubris* Zett. nests in Irish plantation woods

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ABSTRACT. 1. Estimates of worker populations of *Formica lugubris* Zett. nests in Irish plantation woods were obtained using capture–mark–recapture methods. Forager numbers were estimated by paint-marking individuals on the foraging routes and 'recapturing' by traffic counts. Colony-size was estimated using Stradling's (1970) $^{32}$P-radiolabelling technique. Worker brood was estimated by excavation and direct count.

2. Forager numbers ranged from 6906 to 64 686 (eleven nests), colony-size ranged from 9797 to 71 052 (five nests) and worker brood ranged from 9809 to 16 269 (four nests).

3. Forager number was highly correlated with the average traffic on individual routes and the nest forager populations declined rapidly in >30-year-old nests.

## Introduction

There is an extensive literature on the importance of wood-ants in the control of forest pests, though much of the work has concentrated on a single species, *Formica polyctena* Först. (cf. Cotti, 1963; Adlung, 1966). However, there are very few reliable figures for colony-size and forager number in these species and this precludes a precise evaluation of the role of wood-ants. Hence, there is an obvious need for a routine method of estimating forager number, at least. It is also possible that information on the population biology may point to differences between the species in this group in which morphological differences are often obscure (Yarrow, 1955).

The first estimates of colony-size in wood-ants appear to have been made by Forel (1874) who counted a colony during migration to a new nest site. Yung (1900) made total counts of five nests. Holt (1955) estimated forager number in a *F.aquilonia* Yarrow nest from the relationship $N = IT$, where $N$ = the forager number, $I$ = the number of ants completing their journey every unit of time, and $T$ = the harmonic mean of the journey time of all foragers. This method was also used for *F.polyctena* (Horstmann, 1975). However, the journey time of individual foragers seems highly variable and this limits the general application of Holt's method.

Kruk-de Bruin *et al.* (1977) estimated colony-size and forager number by capture–mark–recapture (CMR) in thirteen laboratory nests and two field nests of *F.polyctena*. They marked samples of foragers either with paint or tags of fine copper wire and 'resampled' by making traffic counts of foragers as they passed through a barrier which restricted access to the foraging field to one opening. Their field data are discussed below.

The purpose of this paper is to report CMR estimates of forager numbers, colony-size and worker brood number in field nests of *F.lugubris* Zett. in Irish plantation woods. The method of forager estimation makes use of the route fidelity (Rosengren, 1971) of individual foragers which allows each route to be considered as a separate entity for CMR.

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## Materials and Methods

*Study nests*

Colony-size, forager and worker brood number were estimated in five nests (series 1) which represented the size variation in Irish plantations (Table 1). Since tree age and nest size are correlated (Breen, 1979), the nests probably represent the age spectrum also. The observations were made during 1975 as follows: forager estimates during early July, worker brood on 19 July, and colony-size during the first week of August. Forager estimates were also made at another six nests during 1974 and 1975 (series 2). All observations were made in the Forest & Wildlife Service woods in Tipperary (Breen, 1977). Maps showing nest locations were included in Breen (1976) and voucher specimens are in the National Museum, Dublin.

TABLE 1. Some characteristics of the series 1 study nests

| Nest | Basal diameter (m) | Tree age (years) | Alatae produced in 1975 |
|---|---|---|---|
| GG-936d | 0.35 | 8 | No |
| GG-936b | 0.23 | 8 | No |
| KC-457a | 1.24 | 18 | Yes |
| KC-441a | 0.48 | 30 | Yes |
| KC-452b | 0.47 | 12 | Yes |

*Paint marking*

Foragers were taken from the foraging routes 1–2 m from the nests. In the series 1 observations the foragers were counted into plastic basins, with Fluon-coated sides, and sprayed from 25 cm with Humbrol model aircraft paint. The ants were transferred to a second basin for 15 min, checked for mortality or excessive paint (*c.* 5%) and released on top of the nest. For the series 2 estimates the foragers were marked individually on the gaster with spots of paint, retained for 20 min and released as before.

*Traffic counts*

The number of marked and unmarked foragers was recorded in traffic counts on all routes of the nest, 1–2 m from the nest, 5 min to each route. Counts started 24 h after marking and I aimed at completing ten counts at each nest during the next 2 weeks.

*Radiolabelling and detection*

The radiolabelling technique described by Stradling (1970) was used for the colony-size estimate. This is based on an internal $^{32}P$ mark and it is necessary to starve the labelled ants to prevent transfer of label during food exchange in the colony. Preliminary experiments were done to demonstrate uptake and retention of the label, the number of days starvation necessary and the length of exposure required for adequate detection on X-ray film. Based on the results of the experiments, the following procedure was adopted:

1. Samples of ants were removed from nests, avoiding bias by taking them from various parts of the nest including up to 0.5 m into it.
2. The samples were hand-sorted and counted.
3. The ants were kept in Fluon-coated basins and fed on radio-active solution: 0.5 mCi $^{32}P$ (orthophosphate, The Radiochemical Centre, Amersham) in 5 ml of 25% honey-water at the rate of 0.1 ml to each 100 ants on each of two days, applied to cotton wool. On day 3, 1 ml of non-radioactive honey-water was placed on the wool to increase availability of the radiolabel.
4. All food removed on day 4.
5. After 3 days starvation the ants were replaced on top of the nest.
6. 24 h later the nest was resampled as in (1), handsorted as in (2),
7. anaesthetized with carbon dioxide and autoradiographed on Kodirex X-ray film (Kodak, London) for 10 min. Anaesthesia was maintained by sealing the container with cling film and allowing a slow stream of $CO_2$ to pass through.

It was possible to process 600 ants $h^{-1}$ through the slow stages (2 and 6) and *c.* 500 on each sheet of X-ray film (A-4 size).

*Estimation*

Estimates of forager number and colony-size were made using the unbiased formula of

Bailey (1952):

$$\hat{N} = \frac{M(n+1)}{(m+1)} \text{ with variance,}$$

$$\text{var}\,\hat{N} = \frac{M^2(n+1)(n-m)}{(m+1)^2\,(m+2)}$$

where $\hat{N}$ = the population estimate, $M$ = the total number marked, $n$ = the number of ants in the second sample, and $m$ = the number of marked individuals in the second sample. Where traffic counts formed the 'recapturing' method the second sample was the summation of the observed counts.

*Worker brood estimates*

The number of worker larvae and pupae was estimated by measuring the volume of the brood and counting a sub-sample (0.6 litre) at each of the series 1 nests. However, at one nest the brood was not concentrated in a brood centre on the sampling date (19 July) or within the next 2 weeks and no estimate was obtained.

## Results

*Marking methods*

Laboratory observations showed that the marks were retained for at least 2 weeks. This may be due to the paint adhering to the hairs of the gastral tergites. Kruk-de Bruin *et al.* (1977) mentioned that loss of marks was more rapid in *F.polyctena*, a species much less hairy than *F.lugubris*.

The effect of marking with radioisotopes is not often considered as it can be difficult to measure. However, the route fidelity of 375 foragers marked with $^{32}P$ as above was not significantly different from a control (methods after Rosengren, 1971; $\chi^2_{(1)} = 1.62$, N.S.).

*Population estimates*

Estimates of the number of foragers on thirteen routes of ten different nests are given in Table 2. At two nests (MW-267a, KC-451h) the number of foragers was estimated on two routes of the same nest; otherwise the estimate was made on one route per nest. In the case of one nest (KC-451h) an estimate was made in two successive years. In all cases the proportion of forager traffic on the CMR-studied route(s) was known and the estimate of total nest foragers (Table 2) was based on this. At nest KC-441a, a nest with only two foraging routes, a very low route fidelity (cf. Rosengren, 1971) of 63% was observed; hence the traffic count results were pooled and the forager population was estimated directly from the CMR formula.

TABLE 2. Forager numbers (± SD) estimated using the capture–mark–recapture method. The terms of the CMR formula are explained in the text.

| Nest | $M$ | $m$ | $n$ | Route foragers | ±SD | Total foragers | Average 5 min count of CMR-route | Average 5 min count of total forager traffic |
|---|---|---|---|---|---|---|---|---|
| GG-936b[1] | 250 | 42 | 413 | 2407 | 345 | 10465 | 41.3 | 179.5 |
| MW-267a | 325 | 16 | 75 | 1453 | 302 | 12452[2] | 59.0 | 253.5 |
| MW-267a | 375 | 10 | 148 | 5080 | 1411 | | 74.0 | |
| GG-936d[1] | 200 | 18 | 287 | 3032 | 655 | 6906 | 71.7 | 163.4 |
| KC-440g | 555 | 100 | 1032 | 5676 | 534 | 24895 | 103.2 | 452.6 |
| GG-902c | 900 | 136 | 1079 | 7094 | 564 | 38345 | 107.9 | 584.7 |
| KC-438b | 375 | 50 | 1234 | 9081 | 1233 | 34011 | 137.1 | 513.4 |
| KC-452b[1] | 400 | 53 | 1517 | 11244 | 1489 | 27159 | 151.7 | 366.5 |
| KC-451h | 500 | 91 | 2012 | 10940 | 1108 | 45056[2,3] | 182.8 | 988.9 |
| KC-451h | 500 | 141 | 4212 | 14834 | 1220 | | 382.9 | |
| KC-451h | 569 | 77 | 2402 | 17530 | 1940 | 64686[4] | 240.2 | 887.5 |
| KC-457a[1] | 1000 | 168 | 3252 | 19249 | 1437 | 59594 | 325.2 | 1006.3 |
| KC-441a[1] | 750 | 135 | 4601 | 25379 | 2136 | –[5] | –[5] | 460.1 |

[1] Series 1 nests. [2] Total foragers estimated from route forager estimates of two routes at the same nest. [3] Estimate during 1974. [4] Estimate during 1975. [5] Data from two routes with low route fidelity considered together (see text).

TABLE 3. Estimates of five *F.lugubris* colony populations using the capture–mark–recapture method. The terms of the CMR formula are explained in the text.

| Nest | *M* | *n* | *m* | Colony size | ± SD |
|---|---|---|---|---|---|
| KC-457a | 1646 | 1294 | 29 | 71052 | 12613 |
| KC-441a | 1486 | 2265 | 84 | 39615 | 4191 |
| KC-452b | 893 | 2124 | 54 | 34502 | 4551 |
| GG-936b | 946 | 1067 | 55 | 18042 | 2326 |
| GG-936d | 785 | 648 | 51 | 9797 | 1291 |

The estimates of colony-size range from 9797 to 71 052 (Table 3). The number of worker brood (larvae and pupae) present in four series 1 nests on 19 July is given in Table 4. I have attempted to estimate the annual worker brood production from the following information: brood was present from the end of May until mid-September (≃ 110 days); the duration of egg-adult in *F.lugubris* is likely to be close to 35 days as in *F.polyctena* (Otto, 1962); annual brood production probably follows a hump-shaped curve (cf. Nielsen, 1972). If we assume that the worker brood number was at the maximum on the sampling date, it is possible, using graph-paper, to obtain an integrated value referred to as the 'corrected' brood number in Table 4. The values range from 9809 to 16 269.

A comparison of these results is made in Table 4. The forager ratio was fairly consistent at each nest. The only comparable data based on field nests is that of Kruk-de Bruin *et al.* (1977) who reported % foragers in *F.polyctena*, viz 44% in one nest and two estimates of 48% and 58% for a second nest. The relationship between colony-size and forager number in *F.lugubris* is best fitted by a linear regression (Table 5; Fig. 1). However, the points also plot very closely to the three points given for field nests of *F.polyctena* by Kruk-de Bruin *et al.* These authors applied a log-log regression ($\log_{10}$) to their data and for comparison a similar regression has been fitted to the present data for *F.lugubris*. The result is: *F.lugubris*, log (forager number) = 1.102 log (colony-size) − 0.606, with $r$ = 0.989 ($P < 0.01$), which is very similar to that given for *F.polyctena*, log (forager number) = 1.01 log (colony-size) − 0.75 (from Kruk-de Bruin *et al.*, 1977).

The regression between colony-size and brood number, with only four available points, is not significant (Table 5). However, the % brood in the two small, immature nests is relatively much higher than in the two

TABLE 4. Some population parameters of five *F.lugubris* colonies. The 'corrected' brood estimate was calculated as described in the text.

| | Nest | | | | |
|---|---|---|---|---|---|
| | GG-936d | GG-936b | KC-452b | KC-441a | KC-457a |
| Colony estimate | 9797 | 18042 | 34502 | 39615 | 71052 |
| Forager estimate | 6906 | 10465 | 27159 | 25379 | 59594 |
| Worker brood | 4536 | 6648 | 5170 | 7590 | * |
| Corrected brood | 9809 | 14343 | 11511 | 16269 | * |
| Per cent foragers | 70.5 | 58.0 | 78.7 | 64.1 | 83.9 |
| Per cent brood | 46.3 | 36.8 | 15.0 | 19.2 | * |

* No data.

TABLE 5. Linear regression equations relating some of the population estimates and other parameters

| *x* | *y* | No. of points | *r* | Equation | *P* |
|---|---|---|---|---|---|
| Colony-size | Brood | 4 | 0.571 | – | N.S. |
| Colony-size | Total foragers | 5 | 0.989 | $y = 0.870x - 4210.8$ | <0.01 |
| Nest diameter (m) | Total foragers | 11 | 0.646 | $y = 31708.5x + 5491.0$ | <0.05 |
| Total 5 min count | Total foragers | 11 | 0.942 | $y = 58.63x + 508.6$ | <0.001 |
| Tree age (years) | Nest diameter (m) | 11 | 0.708 | $y = 0.024x + 0.224$ | <0.02 |

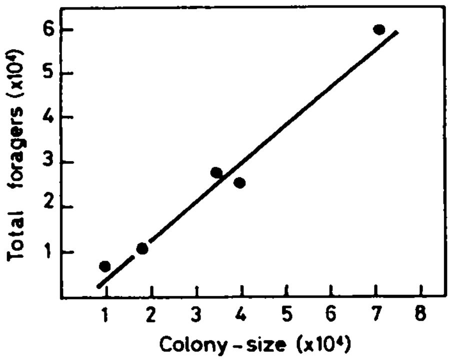


FIG. 1. The relationship between colony-size and total forager estimate. The equation is in Table 5.

mature nests (Table 4), perhaps because the relative investment in worker brood is higher in young nests.

The relationship between forager number on a route and traffic density was highly significant (Fig. 2). Subsequent observations made in Norway (unpublished) suggest that this graph can be extended to include other *F.rufa*-group species. There is also a strong

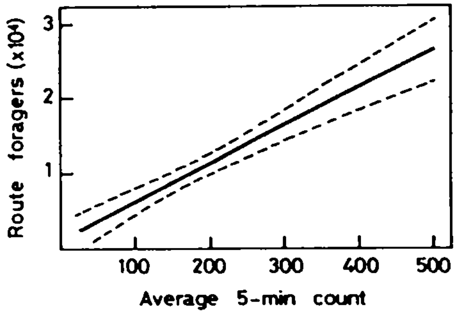


FIG. 2. The relationship between the average 5 min forager traffic on a route and the estimate of route foragers. The equation is $y = 51.17x + 1031.60$, $r = 0.941$, and the broken lines represent 95% confidence limits.

positive correlation between total nest forager traffic and the estimate of total foragers (Table 5). These relationships should allow rapid and consistent forager estimation and further field data are being collected to test their general applicability.

Nest diameter was a less useful predictor of forager number though the regression was significant at the 5% level (Table 5). Tree age was significantly correlated with the nest diameter of the eleven study nests (Table 5) and this is in keeping with the suggestion that nest age and tree age are related. When the forager number and tree age are plotted together (Fig. 3), it is interesting to note a

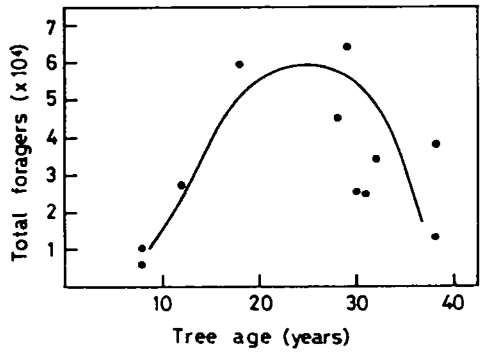


FIG. 3. The decline in forager number in nests located in older tree stands. (Line fitted by eye.)

decline in the forager number at tree age greater than *c.* 30 years.

## Discussion

All the nests studied here were isolated nests. Hence each nest represented a single colony (monocaly), and there were no problems

TABLE 6. Colony-size estimates of species in the *Formica rufa*-group

| Species | Colony-size | No. of nests | Reference |
|---|---|---|---|
| ? | 114000 | 1 | Forel (1874) |
| ? | 19933–93694 | 5 | Yung (1900) |
| *F.yessensis* Forel | 260–51000 | 49 | Ito (1973) |
| *F.polyctena* | 27875 and 139043 | 2 | Kruk-de Bruin *et al.* (1977) |
| *F.pratensis* Retz. | *c.* 60000 | 1 | Jensen (1977) |
| *F.lugubris* | 9797–71052 | 5 | This study |

associated with polycaly (where each colony has more than one nest).

A comparison of the colony-size in *F.lugubris* with that of European wood-ants (Table 6) shows considerable differences within the group (subgenus *Formica*). My data for *F.lugubris* are close to the forager estimate of 59 200 for a large, isolated *F.aquilonia* nest in Scotland (Holt, 1955) and to the series of five wood-ant nests excavated in Switzerland by Yung (1900). In comparison, Horstmann (1975) obtained an estimate of 160 000 foragers in a medium-sized *F.polyctena* nest and suggested that a larger nest with *c.* 3000 forager exits per 5 min would have a forager population of 350 000. My highest forager estimate was 65 000 in a nest with 500 exits per 5 min. In the light of these results, Forel's (1874) claim that large wood-ant nests held up to 500 000 workers appears credible. However, the only colony-size estimates for *F.polyctena*, those of Kruk-de Bruin *et al.* (1977) are somewhat lower (Table 6).

It is not known whether these differences in colony-size are interspecific or caused by environmental conditions. For example, nest and colony-size may vary intraspecifically according to the associated trees (i.e. coniferous versus deciduous woods), or colony-size may be affected by the constant and reliable availability of honeydew-secreting aphids, or the differences may depend on whether the nests are at the limit or optimal part of the species' range.

It is also possible that colony-size variation is due to different numbers of colony queens. Since I have never seen the colony queen in Irish *F.lugubris* nests, it is likely that the nests are monogynic (one queen per nest) or at least oligogynic. It is tempting to suggest that the similar numbers of worker brood recorded in four nests of different sizes and ages (Table 4) are the product of single colony queens. Gösswald (1951) showed that monogynic *F.rufa* L. queens lay at most 300 eggs per day. If egg-laying lasts 110 days the numbers of worker brood (Table 4) can be reasonably considered the offspring of one queen.

Annual cycles of the adult worker population were demonstrated in *Lasius alienus* (FörST.) (Nielsen, 1972) and probably also occur in wood-ants. Thus it should be pointed out that my colony-size estimates were made in early August and would not have included about half of the brood recruited that year to the adult population. The data also suggest an annual worker mortality of *c.* 30% (cf. 50% in *Myrmica rubra* (L.); Brian, 1965).

The decline in forager number associated with tree age, and hence nest age, at about 30 years (Fig. 3) is especially interesting since I have concluded independently elsewhere (Breen, 1979) that nest longevity in Irish plantation woods was between 28 and 38 years. It appears that the foraging population reflects the nests' decline.

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